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Research Article

Plant Feeding in an Omnivorous Mirid, *Dicyphus hesperus*: Why Plant Context Matters

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True omnivores that feed on both plant and animal tissues are not additive combinations of herbivore and predator (carnivore). Because true omnivores must distribute adaptive feeding decisions among two disparate tissue types, understanding the context that plants provide for foraging is important to understand their role in food webs. We varied prey and plant resources to investigate the plant context in an omnivorous true bug, *Dicyphus hesperus*. The contribution of plant species to fitness was unimportant in water acquisition decisions, but affected numbers of prey consumed over longer periods. In plant communities, in the absence of prey, *D. hesperus* moved to plants with the highest resource quality. Unlike pure predators facing declining prey, omnivores can use a nondepleting resource to fund future foraging without paying a significant cost. However, the dual resource exploitation can also impose significant constraints when both types of resources are essential. The presence of relatively profitable plants that are spatially separate from intermediate consumer populations could provide a mechanism to promote stability within food webs with plant-feeding omnivores. The effects of context in omnivores will require adding second-order terms to the Lotka-Volterra structure to explicitly account for the kinds of interactions we have observed here.

1. Introduction

By definition, true omnivores (*sensu* [1]) feed at both plant and consumer trophic levels. However, these animals are not simply additive combinations of herbivores and predators (carnivores) and as such, the rules governing omnivores' use of resources might not be implied from knowledge of the two other feeding types. In addition, physical constraints (i.e., only one type of tissues may be consumed at a time) dictate that these animals must alternate foraging effort between the two types of food. If these two foods are essential, then time and food intake should be budgeted to achieve an optimum ratio of the two resources. Such diet-mixing strategies are well known for a number of herbivores [2]. If the two food types are perfectly equivalent, the omnivore should feed on whichever resource encountered [3]. If the resources are not perfectly equivalent, then the omnivore should employ some form of adaptive foraging rule that will allow one resource to substitute for the other [4, 5]. These rules can range from an increase in frequency of feeding on the less valuable resource as the more valuable declines in profitability, to a step-shaped switch in feeding activity as the profitability of the more valuable resource declines below a critical threshold. However, the rules that have been studied to date were largely those for strict herbivores and predators. It remains to be seen if such simple rules apply to omnivores, given that the aforementioned rules often lack a disparate resource context. For example, predators may choose between different resource types, but these are nutritionally relatively uniform compared to the diet choice of a true omnivore [6].

Plant feeding and prey feeding decisions have important implications for predator-prey dynamics and for energy

flow within food webs [1, 7, 8]. Feeding on high-quality plant parts by omnivores can induce a partial or complete abandonment of foraging for prey, leading to outbreaks of herbivores [9]. In contrast, the increase of omnivore populations on a largely nondepleting plant resource can result in omnivore populations overexploiting prey resources and cause the extinction of those resources [7]. A decline in plant quality (profitability) can result in omnivores increasing their feeding on prey resources, and a decline in prey availability can result in an increase in feeding on plant resources [10, 11]; see [12] for an analysis of the impact of such behaviour on community dynamics. In some omnivorous true bugs (e.g., Heteroptera: Anthocoridae and Miridae), plant feeding also replaces water lost via metabolic functions [13–15] and as such, plant feeding might be considered an essential resource in some omnivore's diets.

Here, we investigate the influence of resource availability and alternate foods as contexts for plant feeding and prey feeding in an omnivore, *Dicyphus hesperus* Knight (Hemiptera: Miridae). This insect feeds on a variety of arthropod prey on several different host plants and also feeds on those host plants [16, 17]. In nature, *D. hesperus* is a generalist with respect to plant host [18] and, presumably, also to insect prey. We have observed it feeding on moth eggs, whiteflies, spider mites, thrips, and aphids in the laboratory. *Dicyphus hesperus* feeds on leaf tissue, even when prey are available [16] and relies on water obtained from feeding on leaves to replenish reserves lost to extraoral digestion [14, 15].

Prey availability and plant feeding influence correlates of fitness in this species as shown in a series of studies that we have conducted [16, 17]. Feeding on prey in the presence of leaf tissue provided an approximately 10% advantage in development time, relative to individuals provided prey with water only [16]. Reproduction and development did not differ among individuals confined to leaves of nine different host plants in the presence of prey [17]. However, in the absence of prey, these nine host plant species had different effects on both development and reproduction of this species with some plant species supporting both development and reproduction and others permitting only brief survival [17]. Taken together, these studies suggest a complex interaction between plant and animal tissue on this zoophytophagous omnivore.

In this paper, we describe a series of experiments that attempt to better understand how and why omnivores respond to disparate resources. We explore the influence of alternative resources within the foraging site (fruits, leaves, and prey) and the background of the plant community. We show that context is in fact, key to developing an omnivore feeding theory and provides some suggestions for further work.

2. Materials and Methods

Laboratory colonies were established using *D. hesperus* collected from white stem hedge nettle, *Stachys albens* A. Gray (Lamiaceae) in the foothills of the Sierra Nevada Mountains at an elevation of ca. 300 m near Woody, CA, USA (Lat. 35°42.9′ N, long. 116°49.1′ W) in 1999. These colonies were maintained at 25.0 ± 0.5°C, 23.0 ± 0.5% RH and a 16 h light (500 μE/m^2/s) and 8 h dark (0.5 μE/m^2/s) diel cycle. *Dicyphus hesperus* were reared on tobacco *Nicotiana tabacum* L. (Solanaceae) with previously frozen *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs provided *ad libitum*. These eggs were sourced from Beneficial Insectary Inc., Guelph, ON, Canada.

2.1. Selection of Plant Tissue. We start with the general observation that, in the absence of prey, *D. hesperus* feeds on tomato fruits and a blemish on the fruit is evidence of that feeding. Feeding on tomato fruits, as opposed to leaves, either confers some fitness advantages to individuals or is evidence of a change in foraging extent. In the latter case, feeding on fruit tissue might result from individuals moving from patches where prey are likely to be found (leaves) in other locations on the plant selected at random. We pursue two lines of evidence: firstly, are there fitness advantages that result from being constrained to feeding on fruit? and secondly, is there evidence that fruit tissue is selected in preference to leaf tissue?

We measured fitness as a tissue-specific function of plant feeding. We accomplished this by measuring survival and oviposition of adult female *D. hesperus* feeding on either tomato leaf or tomato fruit substrates in the presence or absence of prey (eggs of *E. kuehniella*). These experiments were conducted in small cages constructed from 250 mL Styrofoam cups. A 50 mL plastic cup (Solo) was inserted into the larger cup, and the void below was filled with tap water. For exposure to leaf tissue, the stem of single tomato leaf lobe (cultivar Patio) was inserted through a small hole into the water below. The space around the hole was filled with plastic putty to prevent *D. hesperus* adults drowning or accessing water through the opening. For exposure to fruit tissue, a green tomato fruit (cultivar Patio) was placed into the cup. A small hole in the bottom of the Solo cup was filled with plastic putty, and the void below the cup was filled with water, as in the cups with leaves. In prey treatments, *E. kuehniella* eggs were provided *ad libitum* on a 2 cm wide × 1.3 cm deep strip of Post-it note. The cages were kept at 16 h daylength and 22°C and were inspected every 2 to 3 d, and the insect state was determined (live or dead). The water reservoir was refilled and new plant and prey sources were provided at this time, and the number of *D. hesperus* eggs in the plant tissue was counted. This experiment was conducted with 20 pairs of *D. hesperus*. Males were replaced as they died. The 20 pairs were observed in three separate cohorts of 8, 7, and 5 pairs respectively. Age-specific survival and egg production were recorded. Longevity of *D. hesperus* females and total egg production were recorded from these data.

The effects of the above treatments on lifetime reproductive success were determined by calculating Euler's exact r for each cohort and treatment according to the equation:

$$1 = \sum_{0}^{\infty} e^{-rx} lxmx, \tag{1}$$

where x is time and lx and mx are the standard terms for age-specific survival and reproduction. The values of r were

treated as parametric variables and analyzed by a factorial ANOVA with prey availability and plant tissue type as factors.

The effects of plant tissue type and prey availability on egg deposition were determined in a factorial design ANOVA with plant tissue type and presence/absence of prey as the factors. These data were transformed by $\ln(x + 0.33)$ prior to analysis so that the data met the assumptions of ANOVA. A Tukey HSD test was used to discriminate between treatment means. The means and 95% confidence limits (CLs) were backtransformed for presentation. The effect of treatments on longevity of adults was determined by Proportional Hazards Fit (Cox Regression) in JPM 5.1 (SAS Institute, Cary, NC, USA). The effects of plant tissue type were further analyzed by survivorship analysis within each prey-treatment regime.

If feeding on leaf and fruit plant tissue in *D. hesperus* is opportunistic, then individuals presented with the two tissues in a choice setting should express no preference for either tissue. We tested this question in Petri dish arenas (60 cm dia. × 10 cm deep) that controlled the area (amount) of fruit and leaves of tomato (CV Patio) available to starved adult female *D. hesperus*. We measured the frequency of fruit feeding, based on the number of blemishes accumulated on the tomato fruit disc in 24 h. Because feeding on leaf tissue leaves no blemishes or other quantifiable evidence, we were constrained to assess leaf feeding effort indirectly. Fruit and leaf discs were offered in two areas, 50 mm^2 or 12.5 mm^2, and choices were presented as 50 mm^2 pairs, or 12.5 mm^2 versus 50 mm^2 unmatched pairs. Two fruit discs presented together, 50 mm^2 each, provided a measure of fruit feeding frequency when no leaf resource was available. The leaf discs were obtained from young, fully expanded tomato leaves using a cork borer with a 65 mm^2 opening and were cut to avoid major leaf veins. Fruit discs were obtained by using the same cork borer to extract a core from the equatorial plane of green tomato fruits then cutting away the tissue below the margin of the perimeter of the 65 mm^2 disc of epidermis and fruit tissue. The appropriate size was then produced in the arenas using masks of Glad Press'n Seal (The Glad Products Company, Oakland, CA, USA), in which openings of the appropriate sizes were cut. Observation showed that this produced a seal around the perimeter of the plant tissues, and that adult *D. hesperus* were unable to feed through this material. If fruit tissue provided an equal resource to leaf tissue, then the number of blemishes on the fruit should be in proportion to its relative availability in the arena. We calculated a predicted number of blemishes on fruit in each type of arenas by multiplying the number of blemishes present when only fruit tissue was available by the proportion of fruit tissue in the arena. We then subtracted the predicted blemishes from the observed blemishes and, for each proportion of fruit, determined if this difference was different from zero by a Wilcoxon signed-rank test (JMP 7.0).

2.2. Relative Effort of Feeding on Plant and Prey Resources. Omnivores can use the disparate resources in their diet in two fundamentally different ways. They can diet-balance, and thus acquire the two disparate resources in proportions that provide an optimum diet. Alternatively, they can forage adaptively and only feed on the less valuable resource in the absence of the more profitable resource. Previous work on *D. hesperus* suggest that this insect should diet-balance, since it is dependent on water from plants for production of saliva, and thus for extraoral digestion of prey tissue [14, 15]. Plant sap in the diet confers a slight development time advantage compared to individuals provided only water from a wick [16]. Some plant species support development and reproduction of *D. hesperus* and others do not [17].

We used the time allocated to plant and prey feeding following deprivation of these resources to examine the hypothesis that *D. hesperus* uses a diet-mixing strategy to allocate effort to feeding on plant and prey resources. We conducted these experiments on three plant species that have been previously demonstrated to have different profitabilities for *D. hesperus*. We provided prey (*E. kuehniella* eggs) together with one of three plant species for 24 h, followed by 24 h provision of both, either or neither of the resources. The effect of these treatments was subsequently measured by observing the time devoted to plant and prey feeding in a subsequent 2 h observation where both resources were provided. If *D. hesperus* used a diet-mixing strategy in foraging, then we predicted individuals would subsequently allocate time to foraging on the resource that had been absent during treatment. If the profitability of tissue from different plant species affected foraging decisions, then plant species should affect the effort allocated to foraging.

Freshly emerged (<48 h old) adult females were extracted from rearing cages. These were identified by the light coloration of the wings and green coloration of the abdomen. Insects were placed in 50 mL plastic cups (Solo Cup Corporation) with eggs of *E. kuehniella* supplied *ad libitum* on a strip of Post-it note (3 M Corporation, Minneapolis, MN, USA), and a leaf of either chrysanthemum, *Chrysanthemum coronarium* L. (Asteraceae), tomato, *Lycopersicon esculentum* Mill cultivar Rhapsodie (Solanaceae), or mullein, *Verbascum thapsus* L. (Scrophulariaceae). The petioles of the leaves protruded through a hole in the bottom of the cup into a water reservoir below, in order to keep the leaves in fresh condition. These were held in the laboratory at 22°C, with room lighting and a daylength of 12 h. This preexposure ensured that the *D. hesperus* had experience with the plant and prey combination, and that all females within a plant species and prey group were in similar states when the treatment period began.

After 24 h, the insects were transferred from cups containing both leaves and prey to cups containing the experimental treatments. Treatments were without prey/without plant; without prey/with plant (a leaf of the same species as provided in pre-exposure); with prey (*E. kuehniella* eggs *ad libitum* on a Post-it note strip)/without plant; with prey/with plant. As previously, cups with plants had leaf pieces with petioles protruding through the bottom of the cup into a water reservoir, which prevented wilting. These were held for 24 h on a benchtop in the laboratory.

The effects of plant and prey deprivation treatments on the within-leaf feeding responses of individual *D. hesperus* adults were evaluated in arenas constructed from 50 mm plastic Petri plates. Notches were cut in the edges of the

bottom and top halves to accommodate leaf petioles. Leaves of chrysanthemum, tomato, and mullein were cut to fit the inside of the dish. The petiole of each leaf piece was extended outside the dish through a small slot. The petiole was placed into a vial of water to prevent wilting during observation. Prey were supplied in all arenas (50 *E. kuehniella* eggs on a Post-it note strip) and these were placed onto the leaf surface. Insects were moved from the treatment cups into evaluation arenas containing the same plant species as that on which they had been preexposed and treated.

Dicyphus hesperus adults were observed continuously for 2 h. The start and finish times of bouts of plant feeding and prey feeding were recorded with the aid of a stopwatch. Times spent in plant and prey feeding during the entire observation period were calculated by summing the feeding times. A complete set of evaluation trials (including all three plants species and all four deprivation treatments for each) was recorded by two observers (six arenas per observer), and plant species and deprivation treatments were assigned haphazardly to observers. Sinia [19] demonstrated that time spent in feeding and weight of food consumed were highly correlated in *D. hesperus* thus; we, did not weigh prey or plants to determine the mass consumed. The experiment was repeated 15 times.

The effects of host plant species (plant species), access to plant material during treatment (plant deprivation) and access to prey during treatment (prey deprivation) on the times spent in plant feeding and prey feeding during subsequent observation were analyzed in a factorial design, three-way MANOVA (response = contrast) in JMP 7.0. A multivariate approach was required because prey feeding and plant feeding are mutually dependent within subjects, that is, the test subject can only do one thing or the other at any given time. Moreover, many subjects only fed on one resource, meaning that the dataset contained extreme values at both ends of the distribution, and data transformations could not produce a normal distribution. Females that fed on neither resource were not included in either analysis.

2.3. Effects of Plants Species on Predation. We evaluated the effects of plant species on predation. Because omnivores like *D. hesperus* feed on plants to acquire water [14, 15], plant species and their associated differences in biochemistry may not actually provide a context for feeding decisions and foraging effort. Sanchez et al. [17] showed that, in the presence of prey, plant species did not affect development or reproduction so, plants may simply be a source of water and not affect foraging effort or foraging decisions. We evaluated the effects of plant species on prey feeding activity following periods of starvation. The purpose was to determine if plant feeding affected the level of hunger, and thus reduced prey feeding when prey subsequently became available. Female *D. hesperus*, 7 or fewer days old, were placed in small cages with no prey, and a leaf of either chrysanthemum, mullein, pepper, tomato, or a water wick. These females were held, without prey, for 0, 1, 2, 3, 4, 5, or 6 days of starvation. Leaves were replaced if they degraded. Prey (eggs of *E. kuehniella*) were then provided in the cages, on 1 cm wide pieces of Post-it Note, as above, for 7 hours. The number of eggs that were consumed was counted. The data were transformed by $\log 10(x + 1)$ to correct for lack of normality, and analyzed by an analysis of covariance model, using JMP 10.0 (SAS Institute, Cary, NC, USA).

Plant community potentially provides a different context for foraging from that of individual plants. Sanchez et al. [17] showed that life history and reproduction of *D. hesperus* did not differ across plant species in the presence of prey, suggesting that the availability of water to sustain extra-oral digestion may not differ across plant species. However, plants can provide other resources including nutrition, shelter and refuge, and innate expectation of prey. We evaluated the effect of plant community on foraging effort by female *D. hesperus*. Female *D. hesperus*, approximately 7 days old, were starved in 500 mL cup cages, with a tomato leaf, for 48 h, then placed in 65 cm cube cages with a tomato plant ("Rhapsodie," Rodgers Seeds, Boise, ID, USA) and one other plant species—either tomato, mullein or chrysanthemum. Four Postit note strips, each with abundant (>1000) *E. kuehniella* eggs were placed on each leaf of the tomato plant. After five days, we counted the numbers of eggs consumed on each strip and relocated the female. We considered the effects of plant community on two variables: the total number of eggs eaten and the number egg patches visited on the tomato plant. The former was analyzed by a least squares ANOVA. Egg count was transformed to $\log 10(x + 1)$ to correct for lack of normality. The number of visits was analyzed by logistic regression. The experiment was repeated 48 times for each alternate plant species, but we only analyzed data for cages where the female could be relocated at the end of the experiment.

2.4. Adaptive Foraging in the Presence of Prey. Experiments described above demonstrated that *D. hesperus* does not exhibit a preference for tomato fruit tissue over tomato leaf tissue, although being constrained to long-term feeding on tomato fruits in the absence of prey did confer a slight advantage in survival in females compared to females constrained on leaf tissue. In order to demonstrate that feeding blemishes on green fruits on whole plants indicate a change in foraging behaviour that is dependent on the profitability of available resources, we conducted the following experiment. Tomato plants, (cultivar Patio), 12 weeks old, in a peat-based potting mix, in 15 cm pots, were reduced to 4 leaves and 4 green fruit. These were placed in 65 cm by 65 cm cages that were covered with fine cloth. Eggs of *E. kuehniella* on 1 cm wide × 1.3 cm deep Post-it note strips served as prey patches. Three prey treatments were used: high prey, consisting of a patch of >1000 eggs on each leaf; a low prey treatment consisting of a patch of approximately 50 eggs on each leaf; a zero prey treatment. Five female *D. hesperus*, <7 days old, were placed in each cage. After 7 days, the fruit were removed from the plants and examined for feeding punctures, which were counted and pooled across fruit within cages. The experiment was replicated 10 times. Prey availability treatments were compared using a one-way ANOVA, and means were separated using a Tukey test with $\alpha = 0.05$.

Table 1: Mean (upper and lower 95% CL) total eggs laid, lifetime (upper and lower 95% CL) and mean ± SEM, Euler's exact r for female *D. hesperus* on either tomato leaf or tomato fruit, with or without prey (eggs of *E. kuhniella*). $N = 20$.

	Total eggs laid ($N = 20$ females)	Longevity ($N = 20$ females)	Euler' exact r ($n = 3$ cohorts)
Fruit, without prey	1.3 (0.8, 1.9)	17 (10, 23)	0.98 ± 0.023
Fruit, with prey	15.0 (11.8, 19.0)	31 (15, 39)	1.08 ± 0.043
Leaf, without prey	3.0 (2.3, 4.0)	6 (3, 6)	1.21 ± 0.023
Leaf, with prey	41.8 (27.6, 63.1)	28 (4, 50)	1.34 ± 0.037

2.5. Adaptive Foraging for Plant Resources. In the absence of prey, and opportunities to diet-balance, omnivores should feed on the most profitable plant resource available to them within the plant community. We tested this hypothesis using feeding punctures on green tomato fruits on a tomato plant as the indicator of feeding on various resources within cages and in greenhouses. In cage experiments, tomato plants (cultivar Patio) with fruit as above were paired with one of the following plant treatments: a single mullein plant, a single chrysanthemum plant, a single tomato plant (cultivar Rhapsodie), or no other plant. There were no fruit or flowers on any of these alternative plants. Ten females were placed in each cage. The cages were inspected daily and the numbers of insects on the Patio tomato plant was counted. The tomato fruit were harvested and feeding punctures on the fruit counted after 7 days. The sum of the numbers of *D. hesperus* observed on the Patio tomato plants in each cage over 7 days served as an index of the effects of plant community on potential for feeding on tomato fruits by *D. hesperus*. Our *a priori* hypothesis was that the presence of any second plant in the cage would reduce the number *D. hesperus* on the tomato plant by approximately half, and that this would result in a similar reduction in the amount of blemishing on the tomato fruits. There were 7 replicates each of the "none" and "Rhapsodie tomato" treatments and 8 each of the "mullein" and "chrysanthemum" treatments. One replicate of the "none" treatment was lost due to blossom end rot on the fruits. Blemish data were transformed by log base 10 to correct for dependence of the variance on the mean. Backtransformed means and SE values are presented. The effects of prey treatment on numbers of insects on plants and on feeding punctures on fruit were compared using a one-way ANOVA, and means were separated using a Tukey test with $\alpha = 0.05$.

A greenhouse experiment was conducted to further examine the effects of plant community on plant feeding in the absence of prey. Tomato plants, CV Rhapsodie, were grown in hydroponics culture in 4 glass, greenhouse compartments (3.2 by 12 m). These compartments were each split into two, 3.2 by 6 m enclosures with a curtain of Agryl P17 spun bond row cover (BBA Fiberweb, London, UK). There were ten plants in each enclosure, arranged in two rows of five each. These plants had grown to the full height of the trellis wire (3.35 m), and each plant bore approximately 8 trusses of fruit ranging in age from freshly pollinated to near-ripe. There were no prey on any of the plants. In one enclosure in each compartment, a single mullein plant, with a rosette diameter of approximately 60 cm, in a 30 cm hanging basket pot, was placed in the centre of the plants, suspended within the tomato crop canopy. Fifteen *D. hesperus* were released on each tomato plant. The release population consisted of 3 males, 3 females, 3 large nymphs, and 6 small nymphs, which approximated the population age structure in a previous experiment [17]. The numbers of insects on each plant was counted three times during the experiment, on days 3, 7, and 11. After 14 days, all fruit were removed from all trusses on all plants in each house, and the number of feeding punctures on each fruit was counted. Data were recorded by plant truss, numbered from lowest to highest on the plant, in order to also determine if position of fruit on the plant affected the likelihood of that fruit being blemished. Effects of the presence of mullein on numbers of *D. hesperus* on plants were determined by repeated measures (RMs) ANOVA. Effects on the proportion of fruit with feeding punctures were determined by 2-way ANOVA on arcsin (square root x) transformed data, with mullein presence-absence (treatment) and truss number as main effects. Summary data on proportion of blemished fruits are reported as backtransformed lower 95% CL < mean > upper 95% CL.

3. Results

3.1. Selection of Plant Tissue. The intrinsic rate of increase, r, was lower when females were provided fruit tissue than when provided leaf tissue ($F_{1,8} = 54.3939$, $P < 0.0001$, Table 1) and was higher when prey were provided than when not ($F_{1,8} = 12.8684$, $P = 0.0071$). There was no interaction between the factors ($F_{1,8} = 0.2236$, $P = 0.6489$). Female *D. hesperus* laid fewer eggs when on fruit than on leaf tissue ($F_{1,76} = 7.63$, $P = 0.0072$) and more eggs when given prey than when deprived ($F_{1,76} = 57.35$, $P < 0.0001$), and there was no interaction between the factors ($F_{1,76} = 0.19$, $P = 0.6625$) (Table 1). There was an interaction between plant and prey with respect to overall longevity (L-R $\chi^2 = 7.03$, $P = 0.0080$). Therefore, the effect of plant tissue type was analyzed within prey treatment. In the absence of prey, females on fruit lived longer than females on leaf tissue (L-R $\chi^2 = 26.23$, $P < 0.0001$) and in the presence of prey there was no difference (L-R $\chi^2 = 0.14$, $P = 0.7116$). Thus, feeding on fruit tissue in the absence of prey confers a slight advantage in longevity over feeding on plant tissue. There is a disadvantage to feeding on fruit tissue in the presence of prey.

3.2. Plant Tissue Preferences. In Petri dish arenas with different proportions of leaf and fruit tissues available, the

Table 2: Blemishing by *D. hesperus* females on fruit disks of different sizes in Petri dish arenas with different combinations of leaf and fruit tissue available. The observed blemishes on fruit in arenas containing two different tissue types were subtracted from the area-adjusted prediction for blemishes from the arenas with only fruit tissue, and tested by Wilcoxon signed-rank test to determine if this difference deviated from zero. $N = 30$ for all tests.

Fruit area (mm^2)	Leaf area (mm^2)	Blemishes per fruit disk	Wilcoxon test result
100	0	3.57 ± 2.24	—
50	50	1.17 ± 2.08	$P = 0.0054$
50	12	2.96 ± 3.07	$P = 0.44$
12	50	0.87 ± 1.59	$P = 0.33$

Table 3: Results of a three-factor MANOVA (response = contrast) of time spent in plant feeding and time spent in prey feeding by *Dicyphus hesperus* females.

Factor	MANOVA results		
	df	*F*	*P*
Intercept	1, 120	30.50	<0.0001
HOST	2, 120	0.65	0.5237
PLANT	1, 120	10.76	0.0014
PREY	1, 120	26.97	<0.0001
HOST∗PLANT	2, 120	0.53	0.5924
HOST∗PREY	2, 120	0.96	0.3846
PLANT∗PREY	1, 120	7.65	0.0066
HOST∗PLANT∗PREY	2, 120	0.84	0.4334

number of blemishes on the fruit discs was less than expected in arenas with an equal proportion of leaf and plant tissues (Table 2). Otherwise, the number of feeding blemishes on fruit tissue was not different from the number expected. This result suggests that when the two tissue types were equally available, *D. hesperus* females fed more frequently on leaf than fruit tissue.

3.3. Relative Effort of Feeding on Plant and Prey Resources. The resources provided to *D. hesperus* females during the experimental period had a significant effect on the time devoted to feeding on either of the two resources (Table 3). When deprived of prey or plant prior to full access, females spent more time feeding on the deprived resource than when it had been available during the experimental period (Figure 1). There was an interaction between plant and prey access during the experimental period. Females that were deprived of prey, but provided plant, spent relatively less time plant feeding than females in other deprivation treatments (Figure 1). Host plant species did not affect the relative time spent feeding on plant and prey resources following the deprivation period. Thus, there is evidence that *D. hesperus* diet-balances by expending effort to replace the resource that has been deprived.

3.4. Effects of Plants Species on Predation. Plant species affected the way in which female *D. hesperus* responded to prey in starvation treatments (Figure 2, analysis of covariance, Plant host ∗ days of starvation, $F_{4,259} = 2.76$, $P = 0.0281$). The number of prey consumed increased with starvation period for insects confined to pepper, tomato, or water wicks (linear regression, $F_{1,51} = 13.35$, $P = 0.0006$; $F_{1,62} = 10.29$, $P = 0.0021$; and $F_{1,58} = 4.63$, $P = 0.0357$, resp.) whilst prey consumption remained constant over time for insects confined on chrysanthemum and mullein (linear regression, $F_{1,59} = 0.66$, $P = 0.042$; $F_{1,54} = 0.56$, $P = 0.46$, resp.). The average number of prey consumed during foraging bouts was affected by plant species (analysis of covariance, $F_{4,259} = 5.09$, $P = 0.0006$, and Tukey HSD). The number of prey eaten by female *D. hesperus* was significantly greater for insects confined on chrysanthemum (1.47±0.037) than those confined on mullein (1.13 ± 0.074) and tomato (1.22 ± 0.067). The overall numbers of prey consumed on pepper (1.22 ± 0.075) and the water wick (1.35 ± 0.051) were not different from each other or from the extremes.

In the plant community experiment, the species of the alternate plant affected the number of prey eaten ($F_{2,114} = 5.94$, $P = 0.0014$). More prey were eaten when the alternate plant was chrysanthemum (193 ± 28.5, $N = 41$) than when it was tomato (75 ± 1.2, $N = 38$). The number of prey eaten when mullein was the alternate plant (121 ± 25.0, $N = 38$) was not different from either extreme. The number of prey patches that were attacked was affected by the species of the alternate plant (logistic regression, log-likelihood Chi Square = 17.9, df = 2, $P = 0.0001$), and more visits were made to the prey patch when chrysanthemum was the alternate plant that when mullein or tomato were the alternate plants. The females visited the prey patch 2.0 ± 0.21 times when chrysanthemum was present, 1.2 ± 0.17 times when mullein was present, and 0.9 ± 0.15 times when tomato was the alternate plant.

3.5. Adaptive Foraging for Plants in the Presence of Prey. The presence of prey on the leaf reduced the number of feeding

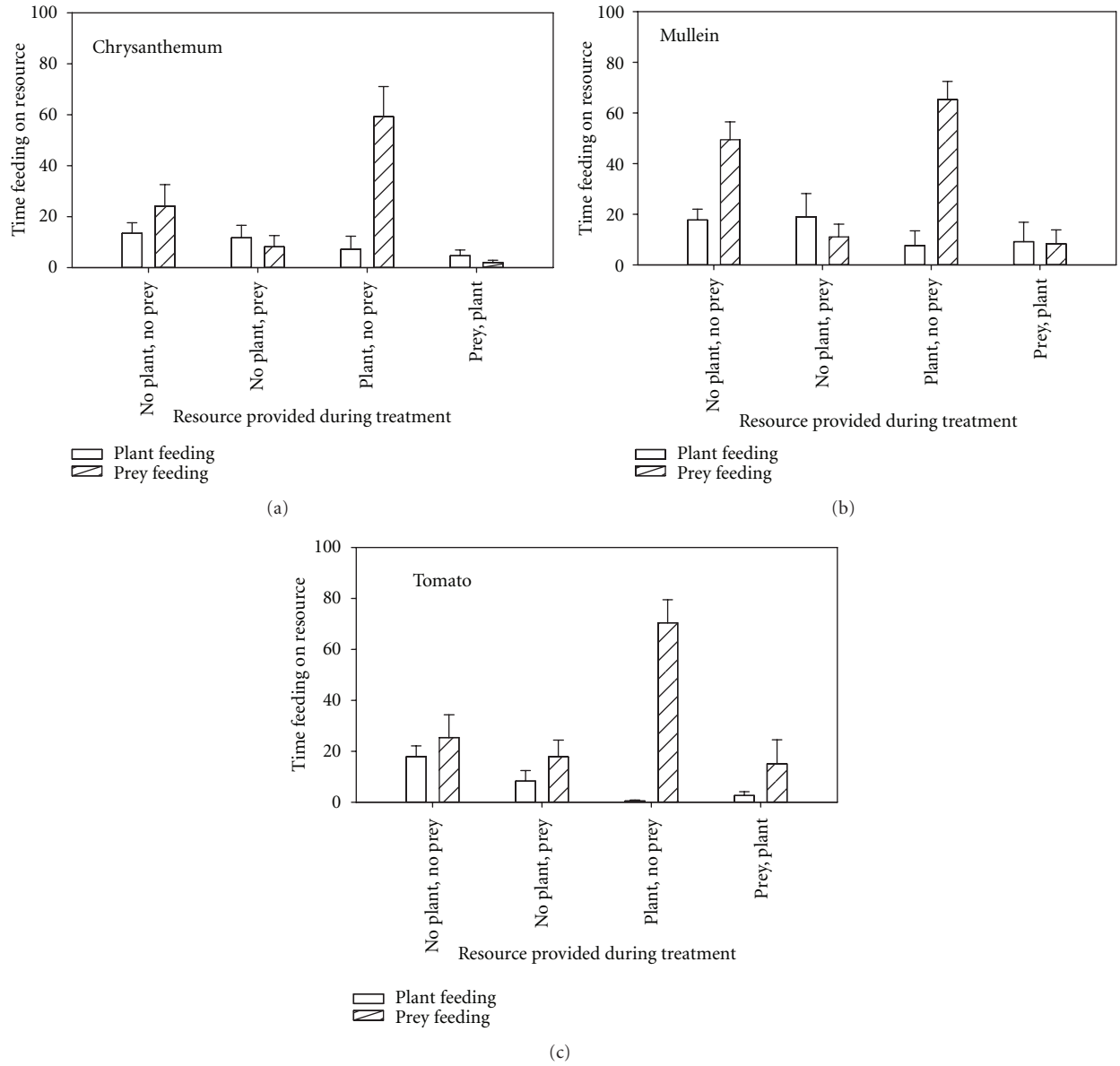

Figure 1: Mean total time spent in (a) plant and prey feeding during a 2 h observation interval and (b) proportion of feeding time that was plant feeding by *Dicyphus hesperus* females after 24 h experimental periods with or without access to plant tissue and/or prey.

punctures on fruit on whole tomato plants ($F_{2,27} = 8.12$, $P = 0.0017$). There were more feeding punctures on fruit in cages without prey (46.8 ± 14.15) than on fruit in cages with low prey availability (3.9 ± 1.42) or high prey availability (5.6 ± 2.65), which were not different from each other (Tukey test, $\alpha = 0.05$). Thus, *D. hesperus* forages adaptively, for the most valuable resource, and the presence of blemishes on green fruit represents a shift in foraging strategy. Interestingly, the presence of even very small numbers of prey on plants was sufficient to keep the insects from shifting to feeding on fruits.

3.6. Adaptive Foraging for Plant Resources. In cage experiments examining the effects of plant community on adaptive foraging for plant resources, experimental run was not a significant effect for either accumulated numbers of *D. hesperus* or numbers of blemishes on fruits ($F_{1,22} = 2.266$, $P = 0.080$; $F_{1,21} = 0.403$, $P = 0.533$). Therefore, further analysis was done without this factor. Blemishing results for one cage were discarded due to disease symptoms on fruit. The accumulated numbers of *D. hesperus* were highest on patio tomato plants paired with no alternative plant, intermediate on Patio tomato plants paired with either chrysanthemum or tomato cultivar Rhapsodie, and lowest on Patio tomato plants paired with mullein (Table 4; $F_{3,26} = 21.722$, $P < 0.001$). Feeding punctures on tomato fruits, however, did not follow the same pattern, and feeding punctures were lowest on patio tomato plants paired with mullein and not different among the remaining combinations (Table 4, $F_{3,25} = 9.611$, $P < 0.001$). These results indicate that *D. hesperus* uses

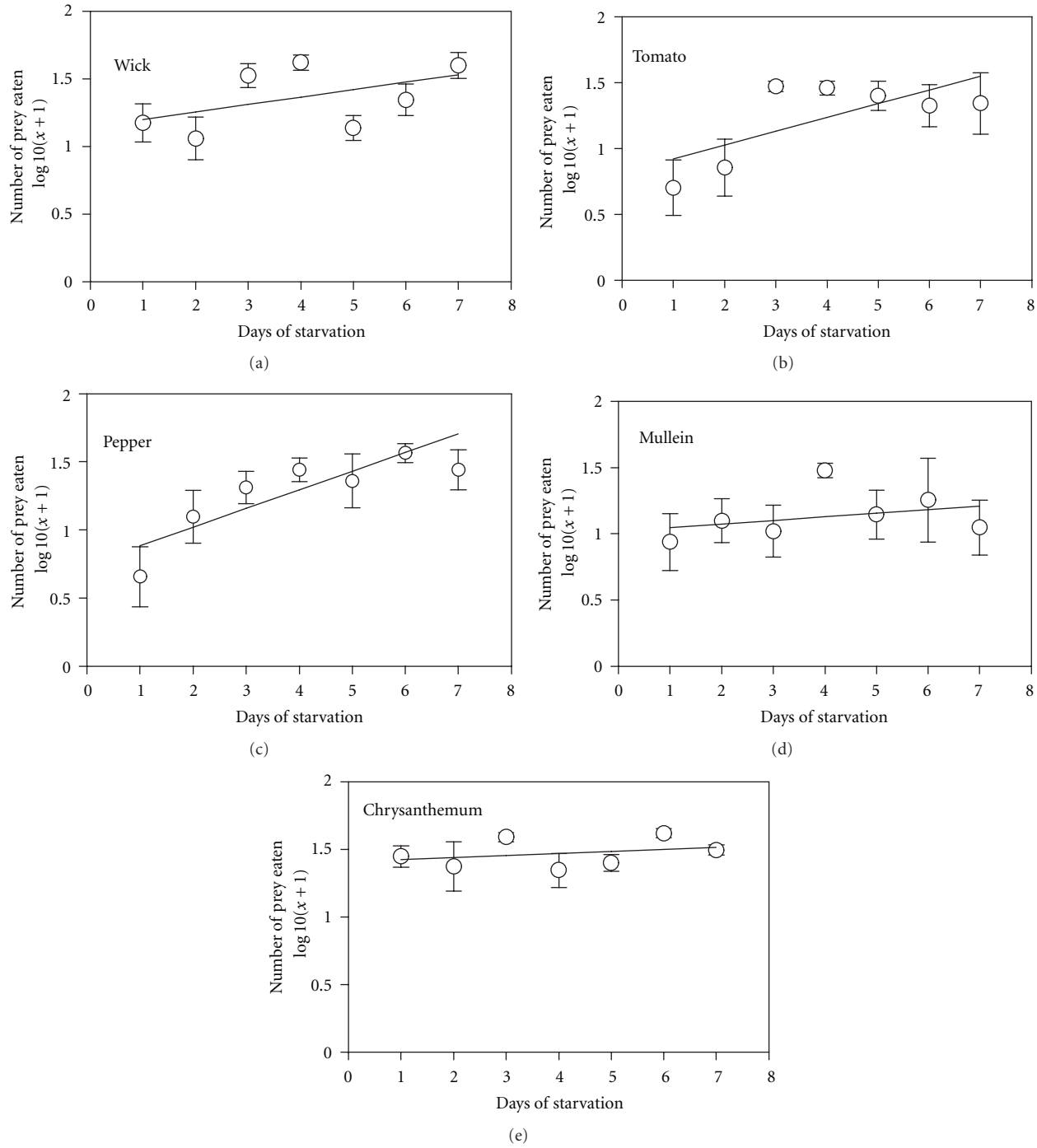

Figure 2: Number of prey consumed by female *D. hesperus* after different periods of starvation while confined to chrysanthemum, mullein, pepper, or tomato leaves, or with a wick providing water. *N* varies from 10 to 3 for each point.

an adaptive foraging strategy for plant species in communities and that it spends time in and devotes plant feeding effort to the plant resource that provides the best fitness returns.

In greenhouse experiments, the number of *D. hesperus* on Rhapsodie tomato plants in greenhouses decreased over time (Figure 3; RM ANOVA, $F_{2,5} = 19.90$, $P = 0.004$), but there was no effect of treatment on the number of insects in greenhouses (RM ANOVA, $F_{2,5} = 1.12$, $P = 0.396$). There was a difference in the proportion of blemished fruit (ANOVA, $F_{1,9} = 8.19$, $P = 0.0059$); the proportion of fruit blemished was $0.012 < 0.023 < 0.038$ in greenhouses with mullein and $0.020 < 0.050 < 0.078$ in greenhouses without. Variance values are backtransformed confidence limits, which are presented because the arcsin (squareroot X) transformation yields asymmetric values for variance. The proportion of blemished fruit varied with truss number (Figure 4, $F_{1,9} = 4.81$, $P < 0.001$), but there was no interaction between treatment and truss with respect to the

Table 4: Mean ± SE (N) accumulated numbers of *D. hesperus* on Patio tomato plants and number of blemishes on fruit in the presence of different alternative plant species. Means in columns followed by the same letter are not significantly different (Tukey HSD, $\alpha = 0.05$).

Alternative plant	Accumulated *Dicyphus*	Number of blemishes on Patio tomato
None	50.3 ± 3.25 a	67.9 ± 5.88 a
	(7)	(7)
Chrysanthemum	35.4 ± 3.61 b	51.2 ± 16.92 a
	(8)	(8)
Tomato (cultivar Rhapsodie)	27.4 ± 2.8 b	43.3 ± 15.70 a
	(7)	(7)
Mullein	12.7 ± 2.7 c	6.2 ± 2.16 b
	(8)	(8)

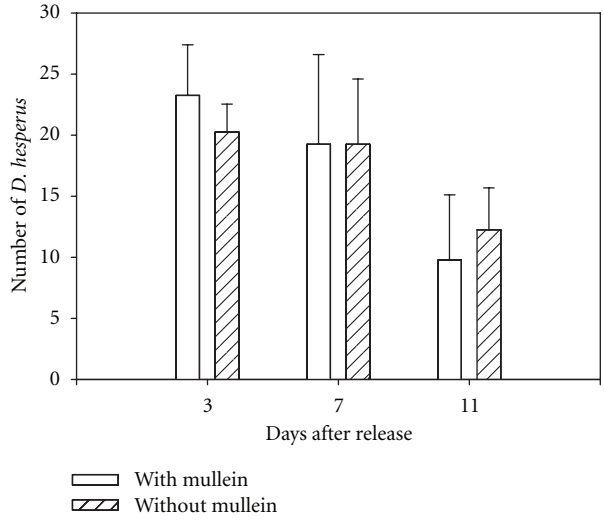

Figure 3: Number of total *D. hesperus* (all stages) on tomato plants in greenhouses in the presence or absence of mullein banker plants and the absence of prey. Values are means ± SE, and $N = 4$ for each bar.

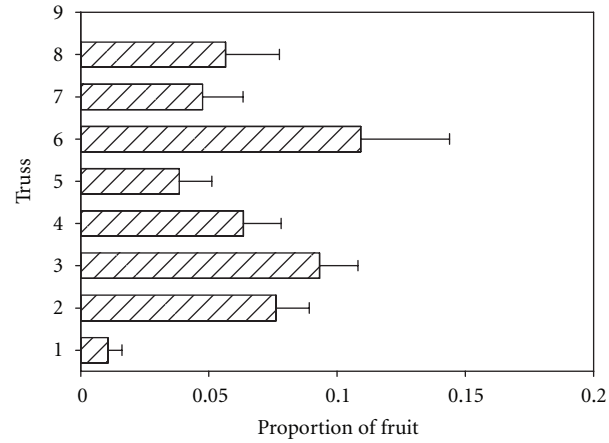

Figure 4: Distribution of blemishing on tomato fruits at different heights (truss 1: low and most mature, truss 8: high and most immature) on tomato plants 14 d after release of *Dicyphus hesperus*' adults and nymphs.

proportion of fruits blemished ($F_{1,9} = 1.07$, $P = 0.3958$). Fruits on the lowest (most ripe) truss were attacked at a lower frequency than other fruits on the plant. These results provide further evidence for the apparent adaptive plant foraging strategy evident in the small cage experiments.

4. Discussion

In the introduction, we posited that true omnivores are not simple, additive combinations of herbivore and predator. As such, both the plant and prey environment should provide context for foraging behaviour and should influence this behaviour in ways that are unique to animals that have an explicitly omnivorous diet. Prey and plant foraging decisions should depend on the specific identity of both the plant and prey resource, and evidence for this context should emerge from the statistical interactions between plant and prey factors in experiments. In fact, our results reveal exactly these interactions and demonstrate that, for true omnivores like *D. hesperus*, the plant context is extremely important. In the discussion that follows, we explore this hypothesis and its implications for arthropod plant dynamics in food webs containing true omnivores.

We assume that true omnivores forage for plant and prey resources according to the rules of optimal foraging theory. Thus, omnivores should forage to maximize fitness and can do so by balancing diet, patch type, or time allocation [20]. A central concept of optimal foraging theory is that, for any finite resource, food intake in a resource patch should decrease with increasing time in the patch due to patch depletion [21]. Patch depletion has an important influence on the evolution of optimization decisions. However, for small, plant-feeding omnivores that inhabit plants and feed on plant tissue (as opposed to pollen or nectar) the plant resource is essentially unlimited and does not readily deplete with feeding. Optimal foraging decisions in these organisms could therefore be made based on depletion of the prey resource and the potential contribution of proximate plant quality to fitness (profitability). In this work, we have not attempted to calculate the optimum behaviours for *D. hesperus* and we use "optimum" in the sense of seeking the best decision providing the highest fitness returns in a qualitative, rather than quantitative sense. Evidence for these

relative fitness returns can be garnered from our experiments here and from previous studies examining the effects of plant and prey diet on correlates of fitness [14, 16, 17].

For *D. hesperus*, the relative contribution of prey species (animal tissue) to fitness is quite similar when contrasted with the contribution of plant tissue [17], and in general, the differences among plant tissue are of greater relative magnitude than differences among prey tissues (e.g., [16, 17] cf. [6]).

In the absence of prey, *D. hesperus* foraged on tomato fruits, which led to an increased lifespan. This might increase the opportunity for the insect to locate additional resources that would support reproduction. However, being constrained to feed on tomato fruit tissue significantly reduced the estimated intrinsic rate of increase, both with and without prey. Therefore, feeding exclusively on tomato fruits could be detrimental to *D. hesperus*. The intrinsic rate of increase is an estimate of the potential profitability of a resource [22] because it measures the effects of the resource on potential population growth. In nature, *D. hesperus* would not be constrained to feed continuously on a resource like tomato fruits, and the short-term gains in longevity might outweigh any incremental losses in reproductive potential if they increase the probability of being able to find prey in the future. In contrast, a pure predator facing declining prey resources does not have the opportunity to use its sole resource (prey) to fund future foraging returns without paying a significant cost. When such resources are in decline, then investment in energy stores would necessarily tradeoff with somatic and gametic investment.

Above we discussed the dual resource exploitation as an opportunity for omnivores; however, such a feeding strategy can also impose significant constraints when both types of resources are essential. When deprived of either plant or prey resources, *D. hesperus* females increased the time feeding on the deprived resource, suggesting that a degree of diet balancing was occurring. However, plant species did not affect the time spent plant feeding. Presumably, *D. hesperus* were primarily replenishing water reserves, and this result suggests that all plant leaf tissues provide similar access to water. This is consistent with the results of Sanchez et al. [17]. The relative time spent in plant feeding across all deprivation treatments was considerably longer than time spent in prey feeding, which reflects the relative contribution of the two resources to fitness.

Based on the lack of effect of plant species on prey feeding following deprivation, we expected that plant species should not affect prey consumption over longer periods. However, plant species did affect prey consumption in *D. hesperus* following longer periods of prey deprivation. When starved for up to 7 days on chrysanthemum, *D. hesperus* ate more prey, when these were provided, than when starved on mullein. Mullein has been shown to provide sufficient nutrition to sustain development and reproduction in *D. hesperus* whereas chrysanthemum does not [17]. Because prey were provided on a common substrate, it is unlikely that plant surface characteristics affected prey consumption. In longer-term consumption experiments in simple plant communities, *D. hesperus* ate more prey and visited more prey patches in communities with chrysanthemum and tomato than in communities with tomato only, reflecting greater effort devoted to foraging when a low-quality plant was present. Overall, the number of prey consumed by *D. hesperus* was determined by hunger, by plant substrate, and by plant community.

The makeup of plant communities also influenced herbivory in *D. hesperus*. In both cage and greenhouse experiments, herbivory on tomato plants in the absence of prey, as measured by blemishing on fruits, was determined by the makeup of the plant community. In particular, the presence of mullein reduced blemishing, relative to monoculture tomato communities and ones with chrysanthemum. This is consistent with the above experiments, which suggest that plant contribution to fitness should be part of adaptive foraging decisions in *D. hesperus*.

Studies on other omnivores foraging for spatially overlapping, complementary resources (e.g., [23]) suggest that as the availability of one resource declines, a dietary shift to the other resource should occur. Western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), reduce feeding on cotton leaves in the presence of spider mites, *Tetranychus pacificus* (Acari: Tetranychidae), and this reduction appears to be a response to reduction in plant quality through induction of plant defense by spider mite feeding on the cotton plant [24]. On poor-quality plants, reproduction and survival of *F. occidentalis* increased as a result of feeding on predator eggs, but on high-quality plants omnivorous feeding had no effects [25]. Plant feeding on cotton by *Geocoris punctipes* occurred in the presence of both high- and low-quality prey, but was greater in increase in the presence of the poor-quality prey [22].

Other omnivorous insects strategically shift feeding efforts based on availability of plant and prey resources. In the presence of high-quality fruit (pods) on soybeans, *Geocoris pallens* reduced predation on aphids [26]. The availability of pollen (a high-quality plant food) to omnivorous mites can reduce predation on thrips and change the distribution of predator mites on leaves [27]. *Dicyphus tamaninii* feed on tomato fruits in the absence of prey [10, 28], but in this species, development of nymphs will occur on tomato fruits in the absence of prey [29]. However, in *D. hesperus*, feeding on tomato fruits may not be an adaptive foraging strategy, if there is no profitability associated with the resource. In addition, *D. hesperus* expresses no preference for tomato fruit tissue over leaf tissue. Therefore, other explanations must be sought for the observed feeding on tomato fruits in the absence of prey. Patch abandonment in *D. hesperus* is influenced by both plant and prey profitability [30]. In our cage experiment, *D. hesperus* could not abandon the patch, since there were no other plant resources in the cage, and plant feeding is essential for survival. The distribution of *D. hesperus* is likely determined by the distribution of its prey, since, at least on tomato plants, the distribution should not be influenced by within-plant differences in plant tissue profitability. Therefore, in the absence of prey it is possible that *D. hesperus* forages for prey on all plant parts. Feeding on fruit tissue may be the result of the insects opportunistically engaging in herbivory while on fruits, as

opposed to deliberately locating themselves on fruits in order to feed. Alternatively, domesticated tomatoes may not confer the same benefits as wild solanaceous plants, but they might provide the same gustatory cues meaning *D. hesperus* may be caught in an ecological trap. The plant and prey communities used in these experiments are quite artificial and derive from our previous work on the application of this species as a biological control agent.

Where plants in communities vary in their direct contribution to fitness and in their actual or potential prey content, omnivores should utilize resources in those communities according to optimal foraging rules, and thus plants should provide context for feeding behaviour in omnivores. Omnivorous insects are known to respond to plant species or quality at the community scale in the presence or absence of prey. Western flower thrips were more prevalent, during migration, in flowers of tomato plants with a high nitrogen status, compared to those with low N status [31]. *Podisus nigrispinus* (Dallas) (Hemiptera: Pentatomidae) forages for a native geometrid on a native plant, guava (*Psidium guajava* L.), in preference to the same prey species on the exotic *Eucalyptus cloesiana* (F. Muell), despite high prey abundance on the latter [32]. Populations of *Orius insidiosus* in fields were higher on bean and corn than on pepper or tomato [33]. The former two crops support development, longevity, and reproduction to a larger degree than the latter two crops [34, 35]. For *D. hesperus*, plant profitability similarly determines where the insects will be located and on what they will feed. This is determined by emigration driven by prey and plant profitability and by the profitability of other available plants in the community (immigration).

In a broader context, true omnivores, that is animals that feed on both plant and prey, use plants in a number of ways, depending on the species and situation. Feeding on plant tissue can top-up prey feeding, can replace prey feeding, or can provide essential nutrients that are required as part of an omnivore diet. The foraging strategies employed by true omnivores to optimize the use of plant and prey resources clearly depend on a plant context. True omnivores that live on plants may feed on the intermediate consumer (e.g., herbivorous prey) available on the plant, can feed directly on the plant part on which prey occur (e.g., leaves), seek out other tissue within the plant, such as fruits, growing points or seeds, or move to other plants or plant species within the community. The stability of communities containing omnivores has been a persistent theme in ecology over the past decade (e.g., [4, 5, 7, 8, 36]), and several theoretical mechanisms have been explored that might promote stability. Křivan and Diehl [5] proposed that stability should be promoted when an omnivore forages adaptively, and the intermediate consumer is the more profitable prey. As the intermediate prey number declines, the omnivore either switches to feeding on the less profitable prey, or broadens its diet, thereby providing the intermediate prey with a refuge from predation. For *D. hesperus*, prey are far more profitable than plants [16, 17] and plant species vary considerably in their profitability [17]. It seems likely that as prey decline in number, and thus patch value declines, the presence of relatively profitable plants that are spatially separate from those supporting intermediate consumer populations would provide a mechanism to promote stability. We suggest that exploring the effects of the context of plants for foraging decisions in *D. hesperus* will require adding second-order terms to the standard Lotka-Volterra structure in order to explicitly account for the kinds of interactions we have observed here.

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